Burying behavior in an Indo-Pacific sea cucumber, *Bohadschia marmorata* Jaeger (Holothuroidea): a circadian, not circatidal, rhythm

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Abstract—Rhythmic burying behavior in a sea cucumber was described and its selective advantage investigated. Two populations of *Bohadschia marmorata* were studied: in a mangrove channel and in a grassflats habitat. Burying was not the result of water depth but rather time of day. In both populations, individuals came to the surface of the sand in mid-afternoon, were most likely to be fully exposed around midnight, and reburied before dawn. Individuals in the grassflats population were more likely to be completely buried during the day, and they emerged from the sand later in the day than the mangrove population. Three hypotheses for the existence of this behavior were investigated: that they bury to avoid (1) exposure at low tide, (2) ultraviolet light (UVB), and/or (3) stingray feeding groups. The timing of the burying rhythm and the lack of a strong correlation between tide and burying support the hypothesis that *B. marmorata* bury to avoid UVB exposure.

Introduction

Sea cucumbers (Echinodermata: Holothuroidea) are major components of the shallow-water fauna in the Indo-Pacific region, but their behavior is poorly known. Kerr (1994) reports 26 species in average densities of 3–4 per m² from Kosrae (Federated States of Micronesia). *Holothuria atra* can reach densities of over 30 per m² (Bakus 1976, Galstoff 1933), with each sea cucumber processing one gram of sand every five to ten minutes (Bonham & Held 1963). Still, basic questions about holothurian behavioral ecology remain unanswered, such as why they are heavily defended (Bakus 1968), what determines their habitat selection, and what triggers spawning. This lack of research is perhaps due to the apparent lack of sea cucumber activity, since their accessibility, abundance, and often individually-unique color patterns make what activities they do undertake easy to study.

One type of sea cucumber behavior that has been studied is covering, or "cryptic" (Francour 1997) behavior. Covering has been reported for sea cucumbers in the genera *Actinopygia, Bohadschia, Holothuria,* and *Stichopus* (Macnae & Kalk 1962, Yamanouchi 1956). Yamanouchi (1956) provided a general description

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of covering behavior from Palau: (1) *Holothuria bivittata* (now *Bohadschia bivittata*), *H. scabra,* and *Bohadschia vitiensis* (since synonomized with *B. marmorata*) bury in the substrate, (2) *Holothuria lecanora* (now *Actinopygia lecanora*) go from moving on grasses to underneath, (3) *Stichopus chloronotus* move from the sand surface to under corals, and (4) *S. variegatus* move from open sand to under grasses. About burying behavior in *B. marmorata,* Yamanouchi discovered two aspects that are not immediately obvious. First, burying individuals feed as they bury but cease feeding while under the sand; later, they ingest sand as they emerge and continue feeding while on the surface. Second, the burying rhythm is endogenous and entrained by light: sea cucumbers keep their rhythm in dark aquaria for several days, their rhythm can be reversed by reversing light schedules, and they bury when exposed to 30 minutes of light at night.

The purpose of this study was to investigate a variety of basic questions about the ecology of burying in *Bohadschia marmorata* Jaeger from the Micronesian island of Pohnpei (7°00′N, 158°10′E). What is the general form of this rhythm, and how much does it vary? Does this rhythm have a circatidal component? How does this rhythm compare between different populations of the same species? What are the major factors that might select for this rhythm?

Bohadschia marmorata range from the Indian Ocean through the Western Pacific (Rowe & Doty 1977). Adults from the populations used here reach 500g (live weight) and are usually a light grey or tan with sharply-defined, dark brown, individually-unique, map-like spots. This species has Cuverian tubules (defensive, sticky tubes released through the anus) and separate sexes. Spawning occurs during day or night in the still water at the peak of extremely high tides (pers. obs.).

In addition to describing the burying behavior of *B. marmorata,* I investigate three factors that may contribute to the evolution of burying behavior: tidal rhythms, sunlight, and predators. Changes in water depth over the tidal cycle may be important for sea cucumbers in shallow water. *Bohadschia marmorata* individuals are found in places where they can be exposed at low tide, and such exposure could impair a variety of physiological mechanisms that require an influx of water—respiration, locomotion, and excretion.

Midday tropical sunshine has the potential to damage sea cucumbers. Having little or no habitat protection from biologically harmful UVB radiation (280–320 nm), burying in the substrate may be the only escape. Other observations also suggest the importance of sunlight for shallow-water sea cucumbers. First, the only species of cucumber around Pohnpei which lives on completely bare sandflats and which does not bury under the substrate, *Holothuria atra,* is also the only completely black species; perhaps such heavy pigment blocks more than just visible light. Second, *B. marmorata* individuals that are above the surface of the sand during daylight hours remain covered with a thin layer of sand as they feed; this fine sand covering is immediately dropped when the sun sets. It has been suggested that sand coverings reflect light and that sand and mucous coverings guard against radiation in *Holothuria leucospilota* individuals exposed at low tide (Bonham & Held 1963). It is possible that sand and other coverings are needed to pro-

tect against UVB underwater also, since UVB can easily penetrate clear shallow water (Jerlov 1950, Kirk 1994). Third, Yamanouchi's (1956) results suggest that *B. marmorata* bury to avoid something rather than obtain a special food, and that they base their burying rhythm on changes in light.

Diurnal burying and other cryptic behavior could be an adaptive response to predation (Francour 1997). Indeed, the numerous defenses of sea cucumbers, such as skin toxins and Cuverian tubules, imply an evolutionary "arms race" with a variety of predators. A list of known and suspected sea cucumber predators (Francour 1997) include those that eat sea cucumbers piecemeal (*e.g.* small crustaceans) to those that ingest them whole (*e.g.,* seastars and fishes). In this study, investigations of whether predation selects for burying are restricted to investigating stingray group foraging. In the grassflats, the stingray *Himantura* prob. *uarnak* (Forsskäl) engages in group foraging as the tide rises, and being one of the most common potentially catastrophic events in the lives of grassflats inhabitants, stingray feeding groups have the potential to kill a large number of sea cucumbers regularly.

Finding that a burying rhythm follows a certain environmental variable does not mean that that part of the environment is what is being avoided. This is especially true of the tide, which may presage or exacerbate other factors. First, if UVB is even slightly reduced by seawater, then increased UVB exposure at low tide is another reason to bury as the tide ebbs. Second, since stingray feeding groups always form when the tide is rising, sea cucumbers may be most likely to bury just after a low tide.

Methods

The populations in this study live around the small island of Temwen, which is connected to Pohnpei proper by a short coral road (Figure 1). Mangrove forests surround Temwen, and natural channels cut through this forest where it grows between Temwen and the main island (Figure 2). One population of *B. marmorata* is located on the West side of Temwen at an intersection of mangrove channels that forms a shallow area about 15m in diameter. The intersection substrate is mostly sandy with small patches of *Halimeda* algae. Almost all *B. marmorata* are located at one end of this intersection where the current is strong between tidal extremes and the substrate firm. This "mangrove population" is isolated by deep channels and reef: by following the fates of ten individuals over several months, it became clear that they are very unlikely to move out of this intersection during their life.

On the East side of Temwen are several hectares of grassflats which stretch between the ruins of Nan Madol on the South, the barrier reef to the East, and a deep channel on the North; this is the location of the "grassflats population." This habitat has a substrate of coral rubble and sand, and deeper areas not exposed at low tide have small corals mixed with grass. *Bohadschia marmorata* is the most common sea cucumber in the shallow grassflats, with *Stichopus horrens* appearing
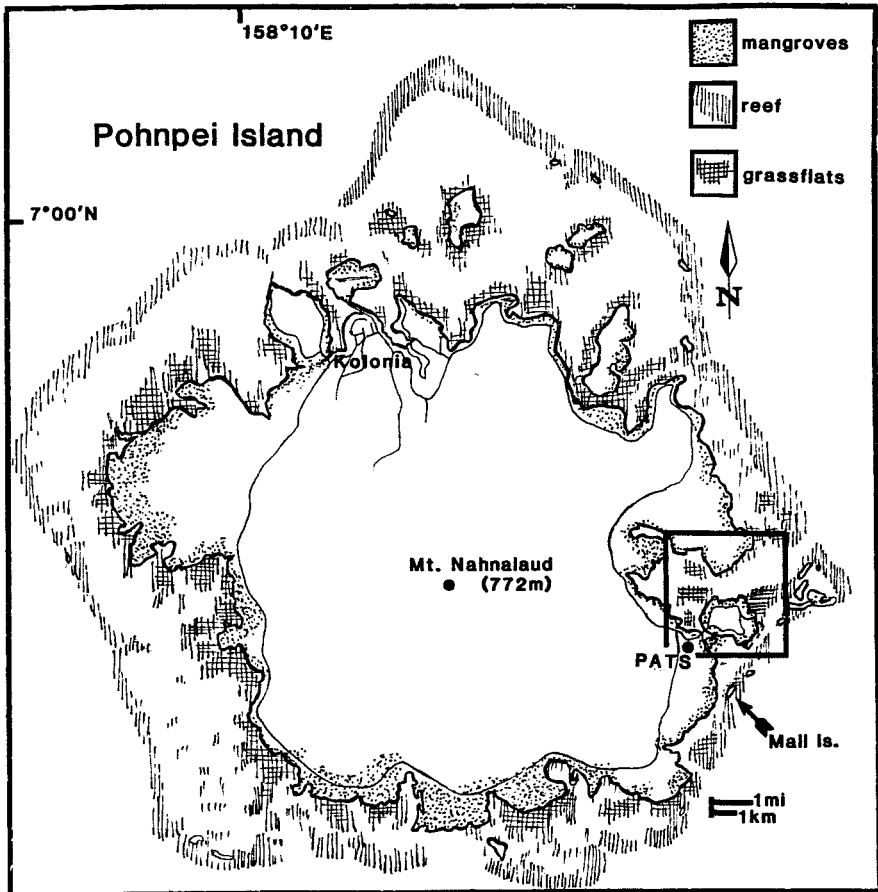
Figure 1.   Pohnpei island, showing location of main study area (box). PATS = Ponape
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occasionally. Adult grassflats individuals are about three times smaller than man-
grove individuals, although their spicules and coloration are identical.

TIME OF BURYING AND WATER DEPTH

In the mangroves, I censused the entire population. In the grassflats, two fixed
2m by 2m plots were censused; one was in the typical grassflats habitat, and the
other was in a disturbed, sandy area sometimes used for coral dredging. For both
populations, each individual in the census area was described as having 100, 75,
50, 25, or 0 percent of its body above the surface of the sand. For those individuals
that were completely buried, I counted them in each census by subtracting the
number of individuals above the sand for that census from the maximum number
ever seen above the sand in that population (79 for the mangrove population, 34
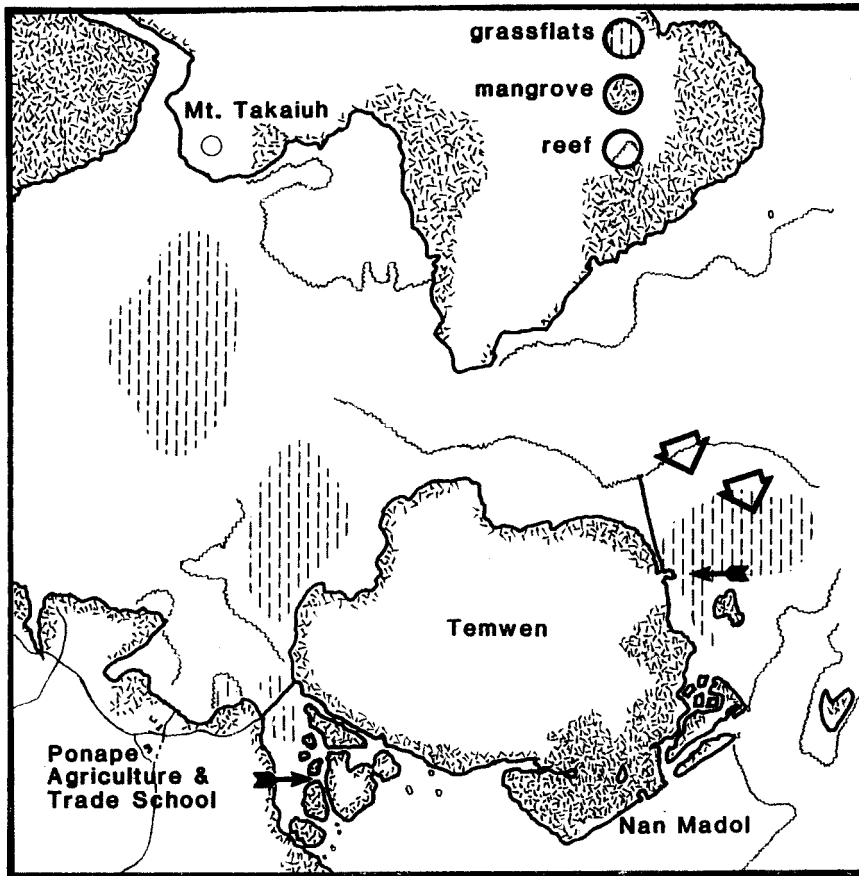
Figure 2.   Detail map of Temwen I. study area. Small dark arrows show mangrove and
        grassflats census populations. Large open arrows show the origin and movement of
        stingray feeding groups.

for the normal grassflats plot, and 10 for the disturbed grassflats plot). This method
relied on the assumption that unseen individuals were buried and not merely in an-
other area. For the mangrove population, this was probably accurate, since the
population was physically contained. For the grassflats population, cucumbers
were free to travel over wide areas, and earlier observations indicated that they
could travel several meters in a day. However, I also observed that they were nu-
merous and distributed evenly at the scale of one or two square meters, so it seems
unlikely that counts of few or none represented situations where there were no cu-
cumbers in the plot.

     For the mangrove population, 35 censuses were made between 24 October
and 31 December, 1994. All censuses were at least 8 hours apart, but most were
more than 24 hours apart. Between 2 and 26 February, 1995, 24 censuses of the

two grassflats plots were taken, each census at least 12 hours apart. Grassflats censuses were taken at the top of an hour (00:00, 01:00, 02:00 . . . 24:00), and for both populations the census time on any particular day was determined randomly. For each sea cucumber on each census, the percentage of their body unburied was plotted versus the time, and third-degree polynomial models were built to compare the populations.

Because I used the same individuals at each census and then pooled the data, the validity of the results may be weakened by the effects of pseudoreplication. Leger & Didrichsons (1994) argue that even when the variation between individuals is higher than for a single individuals, complete data pooling is inconsequential when an equal number of scores is taken from each subject. For the mangrove population, since the whole population was used at each census, this is the case. In the grassflats, however, individuals could enter or leave the plots at any time, so some individuals may have been censused more than once. Thus the condition that all subjects contribute equally to the data pool cannot be guaranteed. Moreover, perhaps individual sea cucumbers have little variation in their daily rhythm but differ greatly from each other; this would increase the chances of an inaccurate grassflats model from data pooling. These problems cannot be answered without a separate study to determine individual variation in burying rhythm, which would require following known individuals. An attempt by me to follow known grassflats individuals had to be abandoned when I could never find them after 24 hours, even when checking 10 meters from their original location. This observation alone suggests that grassflats plots were constantly filled with new individuals, which mitigates the damage of pseudoreplication.

If sea cucumbers bury to avoid exposure at low tide, water depth and percent exposure should be positively correlated. Thus, while collecting census data, I also measured water depth. However, if sea cucumbers bury in close synchronization with the tidal predictors of stingray activity, then they should bury immediately following a low tide. Thus I also noted the depth of the most recent tidal extreme as predicted for Kolonia Harbor.

I also exposed *B. marmorata* individuals to shallow and deep water and measured how quickly each buried. To the mangrove population, I brought two containers, 36cm tall, 113cm in circumference at the base, and 164cm in circumference at the top. In the bottom of each, I put 10cm of sand; one was filled to the top with water, and the other was filled halfway. Between 10 November and 29 December, 1994, I placed pairs of sea cucumbers in the pots. Each pair was matched by size and location in the channel, and each was already buried before being placed in its pot. Each sea cucumber's burial was then timed; if one did not bury, I allowed one hour to pass before terminating the experiment.

STINGRAYS

Stingray feeding groups were first noticed on October 2, 1994, moving over the grassflats area. Visits were made to this area to watch for more groups as time permitted through February, 1995. We looked for groups during all times of the day, especially during census times. If groups started to form, I would position my-

self in the middle of the area and record estimates of group sizes, stingray movements, and the corresponding times until the end of the feeding event, several hours later.

Because of their size and local taboos, killing and dissecting a large number of stingrays was impossible. However, an obvious result of stingrays feeding on *B. marmorata* would be an immediate depletion of sea cucumbers directly behind a passing feeding group. To test for this, I compared the abundance of *B. marmorata* behind and to the side of feeding groups between 11 November, 1994, and 1 January, 1995. A few seconds after a group passed over an area, I censused a circular transect 4m in diameter. Immediately before or after counting behind a stingray group, I used the same method to count individuals in an area 10m to the side of the group.

Non-parametric statistics are used for non-normal data; "±SE" means ±standard error, and "±SD" means ±standard deviation. Burying models were analyzed by calculating 95% confidence intervals for each coefficient; overlapping confidence intervals indicated no significant difference between coefficients.

Results

WATER DEPTH AND BURYING

It became clear by watching *B. marmorata* at night that they do not strongly avoid being exposed at low tide. Often they can be found deflated and stranded on an exposed sand bar, only to continue normal activities after low tide. For both the mangrove and grassflats populations, exposure was not significantly correlated with the water depth at the time of censusing (Table 1). However, exposure was

Table 1. Water depth and depth of most recent tidal extreme versus percent of body above the sand: model equations, R^2 values, and coefficient 95% confidence intervals for mangrove and grassflats populations.

Mangrove Population	
percent exposure = 1.96×10^1 + (1.93×10^{-2}) current water depth + (1.12×10^{-1}) previous tidal extreme depth	
$R^2 = 0.01$	
coefficient	95% confidence interval
1.93×10^{-2}	-6.51×10^{-2} to 1.04×10^{-1} (n.s.)
1.12×10^{-1}	6.69×10^{-2} to 1.57×10^{-1}
Grassflats Population	
percent exposure = 8.72 + (2.02×10^{-1}) current water depth + (1.90×10^{-1}) previous tidal extreme depth	
$R^2 = 0.28$	
coefficient	95% confidence interval
2.02×10^{-1}	-8.47×10^{-2} to 4.88×10^{-1} (n.s.)
1.90×10^{-1}	1.54×10^{-1} to 2.26×10^{-1}

slightly positively correlated with the most recent tidal extreme (mangrove population $R^2 = 0.01$, grassflats $R^2 = 0.28$). In the grassflats population, the model coefficient for the tidal extreme variable (0.19) was significantly larger than in the mangrove population model (0.11). In the test of the effect of water depth on burial rate, the percent of the body buried per minute for sea cucumbers in deep water (x = 0.90 %/min) was not different from sea cucumbers in shallow water (x = 0.91 %/min; p = 0.93; n = 17 pairs; paired t-test).

Timing of Burying

Bohadschia marmorata were most likely to be buried from dawn until mid-afternoon (Figures 3, 4). Table 2 details the 95% confidence intervals for the model coefficients. The model for the disturbed, sandy grassflats plot was not significantly different from the normal grassflats plot and will not be discussed further. The normal grassflats plot and the mangrove population models were very similar; however the "t" coefficient was not different from zero for the mangrove population, and the absolute value of the "t³" coefficient was significantly larger in the mangrove population (2.31) than in the grassflats (1.62). The result was a general lowering of exposure values in the grassflats population, especially during daytime
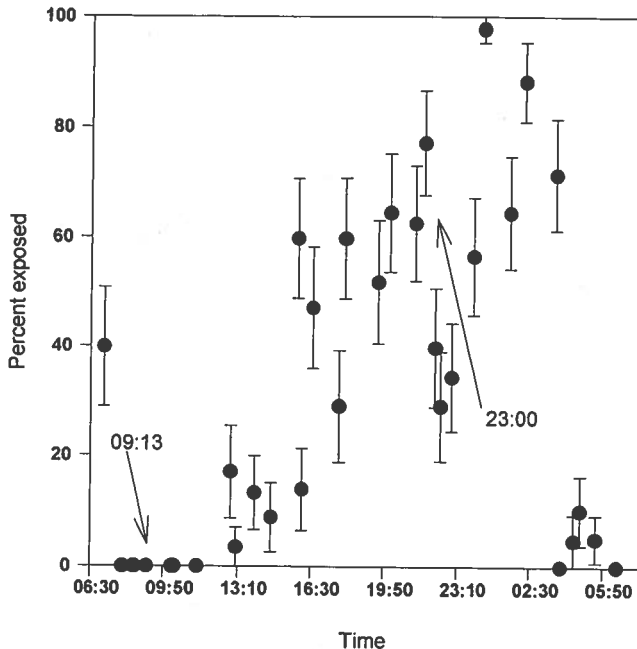

Figure 3.   The percentage of the body above the surface of the
              sand versus time for the mangrove population. The minimum
              (09:13) and maximum (23:00) times, as determined from the
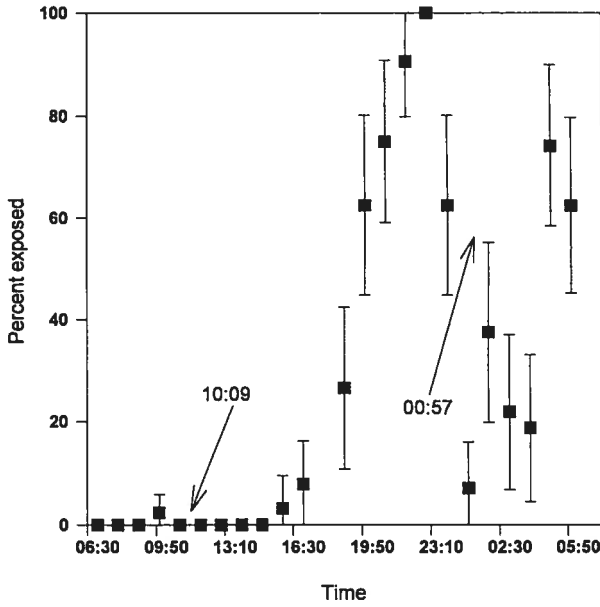   model in Figure 5, are indicated by arrows.

Figure 4.   The percentage of the body above the surface of the sand versus time for the grassflats population. The minimum (10:09) and maximum (00:57) times, as determined from the model in Figure 5, are indicated by arrows.

Table 2.   Time (as number of minutes after 06:30) versus percent of body above the sand: model equations, R^2 values, and coefficient 95% confidence intervals for mangrove and grassflats populations.

Mangrove Population
   Percent exposure $= 7.01 - (1.13 \times 10^{-1})$ time $+$
   (4.02×10^{-4}) time$^2 - (2.31 \times 10^{-7})$ time^3

$R^2 = 0.27$

coefficient	95% confidence interval
-1.13×10^{-1}	-2.37×10^{-1} to 1.13×10^{-1} (n.s.)
4.02×10^{-4}	3.19×10^{-4} to 4.85×10^{-4}
-2.31×10^{-7}	-2.92×10^{-7} to -1.71×10^{-7}

Grassflats Population (Normal Survey Plot)
   Percent exposure $= 7.46 - (1.21 \times 10^{-1})$ time $+$
   (3.29×10^{-4}) time$^2 - (1.62 \times 10^{-7})$ time^3

$R^2 = 0.28$

coefficient	95% confidence interval
-1.21×10^{-1}	-1.28×10^{-1} to -1.13×10^{-1}
3.29×10^{-4}	3.34×10^{-4} to 3.24×10^{-4}
-1.62×10^{-7}	-1.66×10^{-7} to -1.58×10^{-7}

and early evening hours (Figure 5). However, grassflats individuals were more likely to be exposed in the early morning hours. The time of maximum probability of finding individuals above the surface of the sand was earlier (23:00 hours) in the mangrove population than in the grassflats population (00:57 hours).

STINGRAY FEEDING GROUPS

After several dozen attempts to see complete stingray group feeding events, only eight occurences were witnessed in their entirety. All group feeding events occurred as the tide was beginning to rise, and group feeding events were most likely to occur if the tide started to rise before noon (average starting time 10:23AM; range 09:49−14:00; N = 8). Two species frequented the grassflats at this time, *Himantura grantulata* (MacLean) and *H.* prob. *uarnak* (Forsskäl), but only the latter formed feeding groups. About ten stingrays would begin cruising the edge of the exposed grasses while the water was still flowing out, and as soon the current began to change, they started excavating the substrate. Rays would lie alone on the bottom feeding for five to ten minutes before approaching the edge of the exposed grass and other rays. Walking in the water at this time attracted rays: they could be seen changing their course to approach, because their pectoral fin tips came out of the water. After about an hour, up to five groups of two to five individuals would form. At times, these groups would merge and split, and a steady stream of stingrays would enter the grassflats. All individuals would stay in water at least 20 cm deep, but in large groups, some individuals would move out of the water across the backs of others to reposition themselves in the group. Over the course of the next hour, large groups of 20–60 individuals would form, and these would move slowly through the
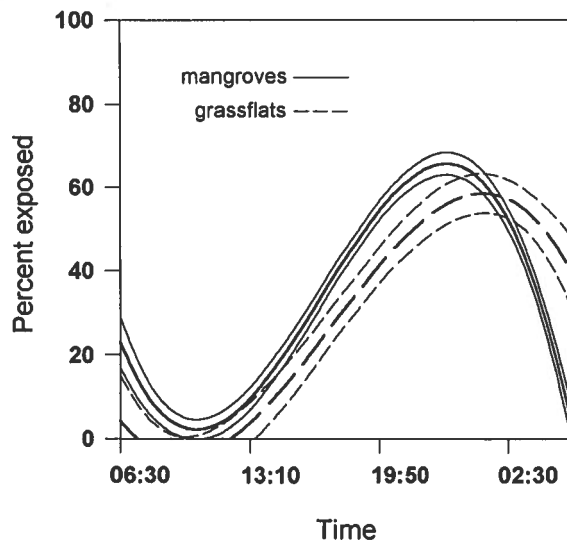

Figure 5.   Burying models, including 95% confidence intervals, for the mangrove and grassflats populations.

shallow water to the Southeast edge of the grassflats, where they would disband. In their wake could be found broken clam shells. Predicting when groups would form was difficult, for on some days of seemingly perfect conditions, no rays were seen.

The number of *B. marmorata* found directly behind stingray groups (x = 2.27 ±SE 0.38) was larger than the number to the side (x = 1.68 ±SE 0.39) (p = 0.05; N = 11 pairs; Wilcoxon).

Discussion

Burying in *Bohadschia marmorata* is clearly a circadian, not circatidal, phenomenon. Moreover, since buried individuals engage in almost no activity under the sand, it seems that they bury to avoid something during the day. Are they avoiding a diurnal predator, the sun itself, or both?

It seems unlikely that *B. marmorata* bury to avoid stingrays. Sea cucumbers do not strongly respond to water depths, a major predictor of stingray activity, and apparently stingrays abandon many (if not all) sea cucumbers removed from the substrate. The higher probability of sea cucumbers to be buried after a low tide, especially in the grassflats, is expected if burying is stingray avoidance. However, this effect is extremely slight: although water depth in the grassflats rarely exceeds 1.5 m, my model requires another 1 m of water at high tide to increase exposure by only 25%. Such a weak but statistically significant correlation may be explained by spawning, in which mature individuals emerge from the sand, at least anteriorly, even during the daytime if the tide is extremely high. On some censuses, then, I may have found an unusually large number of individuals exposed during the daytime because they had just finished spawning after an especially high tide. Although stingrays could be killing sea cucumbers, even if just by accident, it seems now that burying adds little to just Cuverian tubules.

The burying rhythm strongly suggests that *B. marmorata* bury to avoid UVB. The timing of burial insures that they are under the sand during the times of most intense sunlight, especially on the grassflats, where there are no trees to provide protective shade. Sea grasses provide some shade, but their leaves are too narrow to completely cover even the smallest sea cucumbers. In addition, the sun rises over the reef and shines directly on the grassflats as soon as it is above the horizon. In the mangroves, thick foliage and Temwen Island block direct sunlight until mid-morning and after mid-afternoon.

Having no pronounced circatidal rhythm, *Bohadscia marmorata* are unlike many marine organisms that live in or near the intertidal zone (see DeCoursey 1976, Morgan 1991 for reviews). In many ways this is understandable, given that *B. marmorata* rely on a resource that does not change access with the tide (sand), and they apparently can withstand a certain amount of exposure. Some aspects of their behavior show a tidal component, such as spawning, but this was seen only three times during the study.

It has only recently been widely documented that many organisms use biochemicals or behavior to avoid UVB damage (Calkins & Thordardottir 1980, Carlini & Regan 1995, Masuda et al. 1993, Stocha et al. 1994). Moreover, the loss of

stratospheric ozone and subsequent increase in UVB doses has led to a surge of studies on the ecological effects of ozone loss (El-Sayed 1988, Holm-Hansen et al. 1993, Smith et al. 1992, Weiler & Penhale 1994 for a review). The use of phototaxis to avoid UVB has already been suggested for some protists (Calkins & Thordardottir 1980), and this constitutes an important link between ethology and environmental studies in light of concerns over human impact on ozone levels. When present in Holothurians, phototaxis has always been negative (Bakus 1976, Bonham & Held 1963), and *Holothuria captiva* may show signs of stress—releasing Cuverian tubules—when exposed to strong sunlight (Bakus 1976). This study suggests that some sea cucumbers use a circadian rhythm to achieve the same goal as negative phototaxis. For an animal that lives in a habitat that provides few substantial shadows and is exposed to a fairly constant level of UVB throughout the year, reliance on burying controlled by an endogenous rhythm maybe the most efficient and reliable way to avoid UVB damage.

Testing the UVB hypothesis directly is technically difficult, but it should be attempted. During this study, cages were built to house sea cucumbers above the sand during the day. Half of these cages were lined with a UVB-blocking plastic, and half with normal plastic. However, three problems emerged: (1) sea cucumbers were extremely adept at escaping, (2) silt settled on the plastic continually, and (3) the normal plastic became UVB-blocking after a few weeks in the water. However, from what data we did collect, it seemed that individuals exposed to UVB lost more weight, and they developed skin lesions. This failed attempt to test the effects of UVB directly should serve as lesson and encouragement to any future investigators.

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